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Morphological Parallelisms of the Bulla and Auditory Ossicles in Some Insectivores and Marsupials

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ABSTRACT

Insectivores and marsupials show similar phylogenetic stages of morphological differentiation of the tympanic, entotympanic, and the malleus, which range from generalized (*Solenodon-Didelphis*) to the highly specialized (*Tupaia-Dromiciops*). In the insectivores the tympanic process of the basisphenoid takes the place of the tympanic process of the alisphenoid of the marsupials. The presence of an entotympanic suggests specialization in both orders. The malleus of marsupials and insectivores undergoes greater morphological changes than the incus. The ossicular functional axis meets the horizontal in a large angle in the generalized taxa and shows a smaller angle and even a negative one in *Dromiciops* and the burrowing insectivores. Apparently, the malleus turned first, as was also shown for marsupials (Segall, 1969b), other morphological changes followed later. This morphological sequence is probably caused by mechanical influences.

In insectivores the stapes is characteristically and consistently specialized, unlike the two other ossicles, which show far greater differences. The marsupials show a greater range in the shape of the stapes, especially of the plate. Even if the stapes is not preserved, as is usually true in fossil specimens, the fenestra ovalis gives an accurate outline of the shape of the stapes plate and of its position. The shape of the latter or the fenestra ovalis in marsupials varies from practically round to oval in the more generalized and elliptical in the specialized taxa. In the insectivores generalized and specialized genera alike have stapes with elliptical plates.

In the fossorial genera of both orders tympanic, malleus, incus, and the articulation between the latter two are markedly affected. However, the stapes retains the ordinal characteristics.

The stapes of the insectivores has well-curved crura. In most genera the stapedia artery fills only a part of the intracranial space, which speaks for the independence of the two. Thus, it can be assumed that the function of the stapes is the most influential factor for determining its shape.

The round outline of the stapes plate (or fenestra ovalis) is considered the primitive condition, the elliptical the specialized one.

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INTRODUCTION

This is a continuation of my study of the auditory region of mammalia. The previous report deals with the morphology of the bulla, malleus, and incus in marsupials (Segall, 1969b). This study covers the same aspects of the auditory region in insectivores. Both orders show many great morphological similarities in the phyletic stages of the auditory region and some differences. While in the paper on the marsupials only the malleus, incus, and bulla were considered, in this study special attention is also given to the stapes. The stapes, or in fossils in which the stapes is commonly missing, the fenestra ovalis, may be useful in classification. Since the comparisons between the stapes of insectivores and marsupials led to interesting results, a detailed study of certain marsupial stapes is also presented to supplement the description by Doran (1877). In several places probable functional relationships were mentioned, but these have not been studied.

METHODS AND MATERIAL

All specimens were examined under a binocular microscope. When necessary, obscuring bone was removed to expose the ossicular chain. The angle of the ossicular functional axis with the Frankfurter horizontal plane was measured.

The ossicular functional axis is an imaginary straight line running from the tip of the short crus incudis through the incudo-malleolar joint to the upper insertion of the anterior process of the caput mallei.

The lever ratio has been determined and noted in some specimens. It is the length of the malleolar arm divided by the incudal lever arm. The position and the length of the manubrium and long crus incudis are, therefore, of importance for the function of the auditory system.

The long diameter of the stapedial plate and the maximal width perpendicular to this were measured and the ratio between them determined. Since the stapes plate, with the help of the stapedial ligaments, fits snugly into the fenestra ovalis, the contours of the latter give an exact outline of the plate. Therefore, measurements of the fenestra were taken in specimens lacking the stapes. This provides reliable measurements in fossil material where the ossicle is missing most of the time, but the fenestra ovalis is clearly visible. Measurements of the fenestra ovalis were easier to take and for this reason proved even more exact than the measurements of the stapes ratio based on the stapes in place. The results were repeatedly checked

and small differences were often found. The figures arrived at are, therefore, meaningful approximations.

MATERIAL

The following specimens of the recent and fossil mammal collections of Field Museum of Natural History and the American Museum of Natural History (AMNH) were studied:¹

MARSUPIALS

Family Didelphidae:

Didelphis 24154, 96199, 13779, 13783, 56196, 15556; *Monodelphis* 70539, 22182; *Marmosa* 61878, 69833, 69845; *Caluromys* 70994, 68801, 22208, 87927; *Philander* 69805, 70983.

Subfamily Microbiotheriinae: *Dromiciops* 50074.

Family Dasyuridae:

Dasyurus 81523, 42759; *Sarcophilus* 46006.

Family Notoryctidae:

Notoryctes 1061 (AMNH).

Family Peramelidae:

Perameles 60943, 64349; *Echymipera* 56369, 56366, 56368.

Family Caenolestidae:

Caenolestes 81464, 70816.

Family Phalangeridae:

Phalanger 53968, 53970; *Petaurus* 64332.

Family Macropodidae:

Macropus 47318, 44295; *Dendrolagus* 60895; *Aepyprymnus* 47429.

INSECTIVORES

Family Solenodontidae:

Solenodon 57207, 18505, 57068, 51068.

Family Nesophontidae:

Nesophontes 17107 (AMNH), 17108 (AMNH).

Family Tenrecidae:

Tenrec 85512, 21846; *Setifer* 85513, 85170; *Echinops* 33948; *Oryzorictes* 05640, 05637, 05641.

¹ I follow in the main Simpson's classification of mammals (1945) for the general level of organization of the forms studied.

Family Potamogalidae:

Potomagale 72831, 25973.

Family Chrysochloridae:

Chrysochloris 26353, 26352.

Family Erinaceidae:

Echinosorex 68736; *Hylomys* 47113, 46336; *Erinaceous* 57525, 82122, 84448; *Hemiechinus* 74549, 41789, 09719.

Family Leptictidae:

Ictops UC1483.

Family Macroscelididae:

Elephantulus 34040, 38494, 38499; *Nasilio* 16659.

Family Soricidae:

Sorex 41788, 41789, 09719; *Blarina* 15284, 44521, 13152.

Family Talpidae:

Talpa 82581, 23519; *Scalopus* 08156; *Scapanus* 09732; *Euroscaptor* 35406; *Condylura* 28783, 80049, 07071, 21707; *Uropsilus* 36143, 36142.

Family Tupaiidae:

Tupaia 63009, 63020, 63018.

MORPHOLOGICAL REMARKS

As is well known, the embryologic and phylogenetic origin of the stapes differs from that of the malleus and incus. The stapes derives from the hyoid arch, while the malleus and incus develop from the mandibular arch. This is supported by the innervation of the muscles of the middle ear. The tensor tympani which inserts into the malleus belongs to the mandibular arch and is innervated by a branch of the trigeminus. The stapedius muscle is derived from the hyoid arch and is innervated by a branch of the facial nerve.

Doran (1877) divides the marsupials into two groups on the basis of the morphology of the stapes. A small group to which, according to him, *Didelphis* and *Macropus* belong have a small opening between the crura, while the rest have a columella-like stapes.

My observations show that not many genera among the marsupials have a columella-like stapes. The majority have a triangular or somewhat triangular stapes with a small opening between the crura. In some genera the opening is pinpoint sized, in others it is

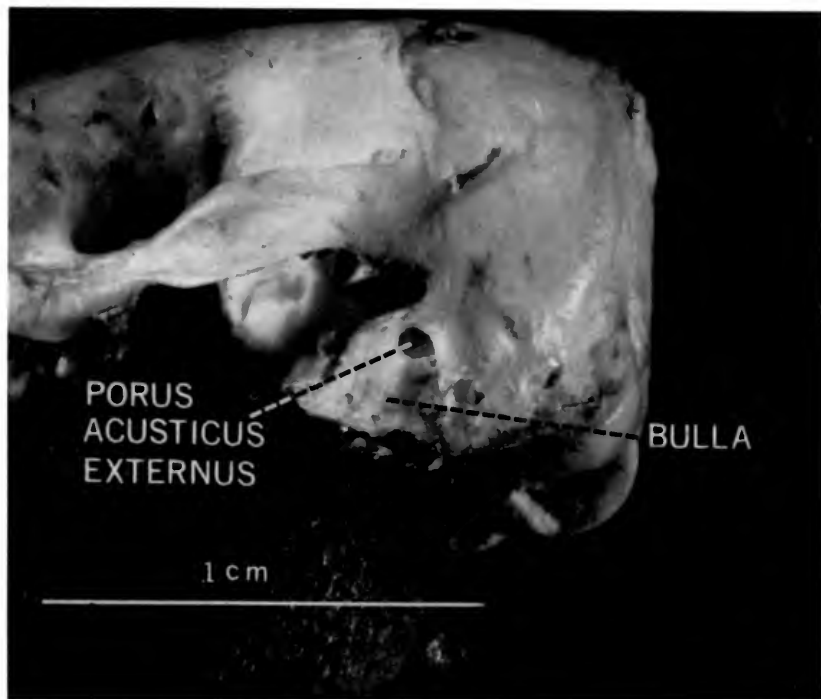


FIG. 1. *Notoryctes typhlops*. Lateral view of the left auditory region.

slightly larger. The term columella-like is used here, although in marsupials the stapes is nowhere near as rod-shaped as it is in monotremes. On cross-section it has an oval (*Dasyurus*) or even flat shape (*Notoryctes*). Toward the base the columella spreads fan-like in the longitudinal diameter of the plate, a condition morphologically intermediate between the columella shape and the typical stirrup of higher mammals. The stapedial plate of the marsupials with a columella-like stapes is about circular or oval. It is more elongated in the various genera and reaches an elliptical shape in the more specialized genera as in *Dromiciops*.

None of the insectivore stapes observed has the columella-like shape, but there is a long elliptical plate in all genera, generalized and specialized alike. Its labyrinthine surface is mostly flat, sometimes convex (*Chrysochloris*, *Elephantulus*). Its crura are much curved and leave a large opening between them through which the arteria stapedia passes. The latter usually fills one-third to one-half of the linear intracural space, but very rarely the whole space. Sometimes

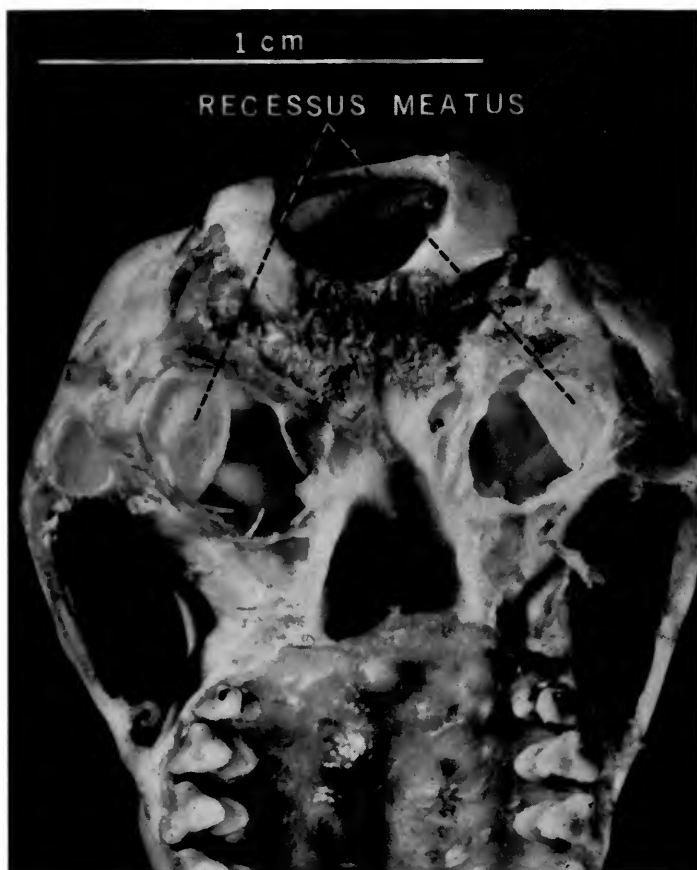


FIG. 2. *Notoryctes typhlops*. Ventral view of the auditory region. (Both bullae broken.)

the artery is enclosed in a bony canal which is sometimes incomplete where the artery passes between the crura (*Chrysochloris*, *Tupaia*). This condition is found in: *Chrysochloris* (*stuhlmanni* ?) 26352, 26353, *Amblysomus leukorhinus* 81730, *Talpa micrura micrura* 82581, *Scalopus aquaticus* 8151, *Scapanus townsendi* 9732, *Euroscaptor micrura* 35406, *Condylura cristate* 28783, *Tupaia palawanensis* 63009. In all other families studied a bony canal is missing.

Notoryctes typhlops

Figure 1

A description of the relevant parts of the auditory region in *Notoryctes* is included here as a skull was not available to me at the time

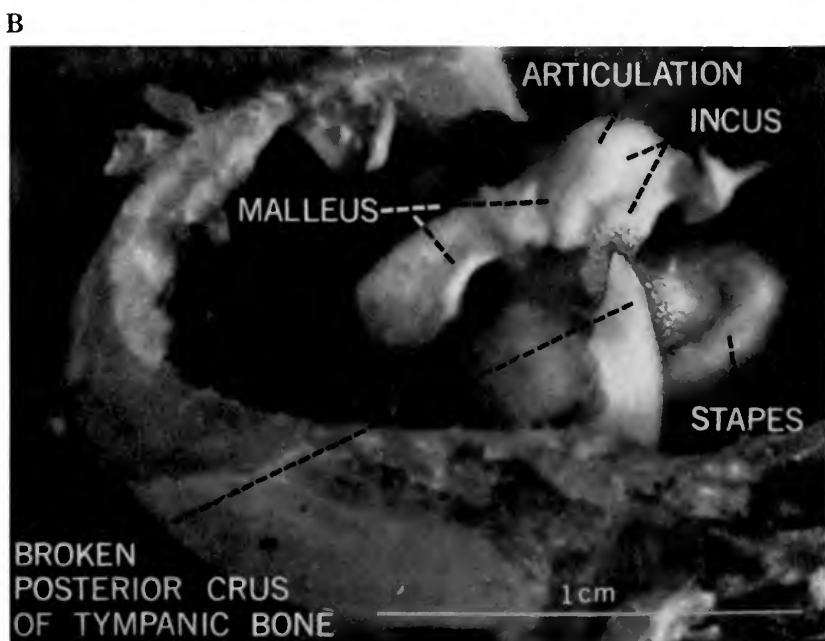
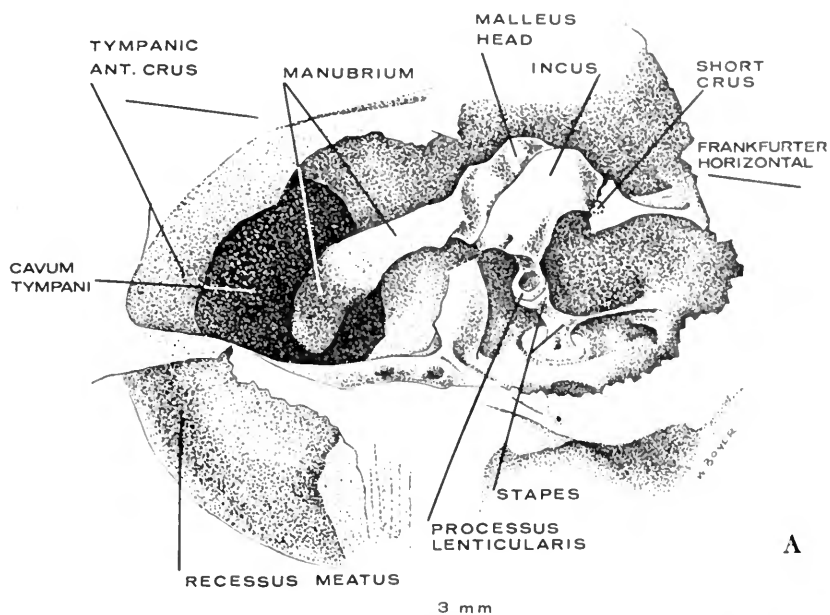


FIG. 3. *Notoryctes typhlops*. A. Lateral view of the left malleus and incus; latero-ventral view of the left stapes. (Obscuring bone removed.) B. Latero-ventral view of left middle ear. (Obscuring bone removed.)

the paper on the auditory region in marsupials was in preparation (Segall, 1969b).

The configuration of the auditory region of *Notoryctes* reminds one very much of that of *Talpa* and *Chrysochloris* (fig. 1). It resembles the latter to such an extent that E. Cope looked upon it not as convergence, but as the result of phylogenetic affinity (Weber, 1928).

A large process of the alisphenoid covers the cavum tympani ventrally. The ectotympanic forms a large recessus meatus which, as in *Dasyurus*, projects into the middle ear (fig. 2). Laterally, the recessus turns in a dorsal direction and forms part of the circumference of the small, oval-shaped porus externus which is similar in appearance to that of *Chrysochloris*. The anterior and posterior crus of the tympanic approach each other closely, leaving a small incisura tympanica open dorso-caudally.

In the specimen studied the ossicles are *in situ* and will be described to the extent that they are visible in that position (fig. 3A, B). No description or illustration of them can be found in the literature.

The shallow head of the malleus is calotte shaped. The line of articulation with the incus is straight and runs from dorsal and slightly caudal to ventral and slightly cranial. It can be assumed that the articulation is even more flat than in the Talpinae and in the Chrysochloridae. The shape of the articulation which differs from all other marsupials, but is similar to that of *Talpa* and *Chrysochloris*, is presumably the result of the modified function of the ossicles in the subterranean genera. A lamina is missing in *Notoryctes*. I suspect the presence of a short neck, although the border between head and neck is ill defined. The manubrium is flat on its lateral side. It has a straight anterior and a somewhat irregular posterior edge. Its distal part, which is slightly wider, is sharply bent medially and its end is rounded.

The body of the incus continues without distinction into the short process, the end of which is pointed and directed caudally. It sits in a small bony cavity which is situated on the edge of a supporting lamina that extends from the medial and posterior wall of the cavity. The flat dorso-lateral part of the stapedial crus incudis is only partially demarcated from the body of the incus by a shallow, short groove. Its delicate, flat, ventro-medial end, which is bent about 90° against the upper part, is slightly concave on its ventral side and articulates through a wide, oval, lenticular process with the identically shaped head of the stapes.

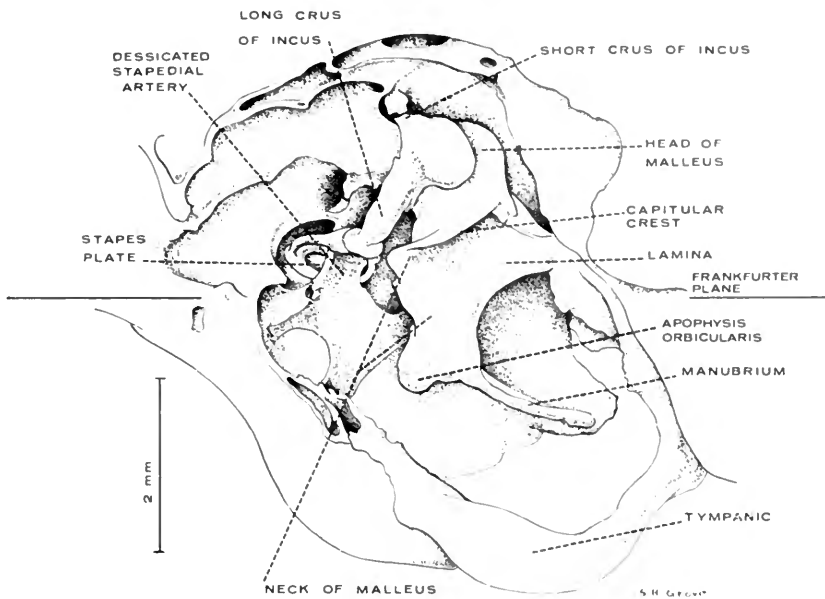


FIG. 4. *Solenodon paradoxus*. Latero-ventral view of right middle ear. (Obscuring bone removed.)

The columella stapedis, which is flat dorso-ventrally, enlarges fan-like in the horizontal plane toward the plate. The stapedial muscle converges into a thread-like tendon, which inserts into the middle of the posterior margin of the columella. There is no arteria stapedia present. A pinpoint-size indentation is visible in the columella near its base and is probably an indication for a foramen. The stapes ratio is about 1.4.

Solenodon paradoxus

Figure 4

The tympanic forms an incomplete ring with the incisura open dorsally. It has a small recessus meatus which widens slightly antero-inferiorly. Its posterior crus is in contact with the tympanic process of the periotic. The ventral side of the cavum tympani is not covered by bone.

The malleus and incus have a generalized structure; the articulation is saddle-shaped; the capitular crest is very distinct and the long neck is sharply bent. The large lamina is quadrangular in shape. The distal end of the neck has a well-developed apophysis orbicularis.

The antero-dorsal and postero-ventral faces of the manubrium are flat and it ends in a slender spatula. The posterior (short crus) is short and reaches into the epitympanic recess. The ossicular functional axis angle with the horizontal is about 32° and the lever ratio is 1.2.

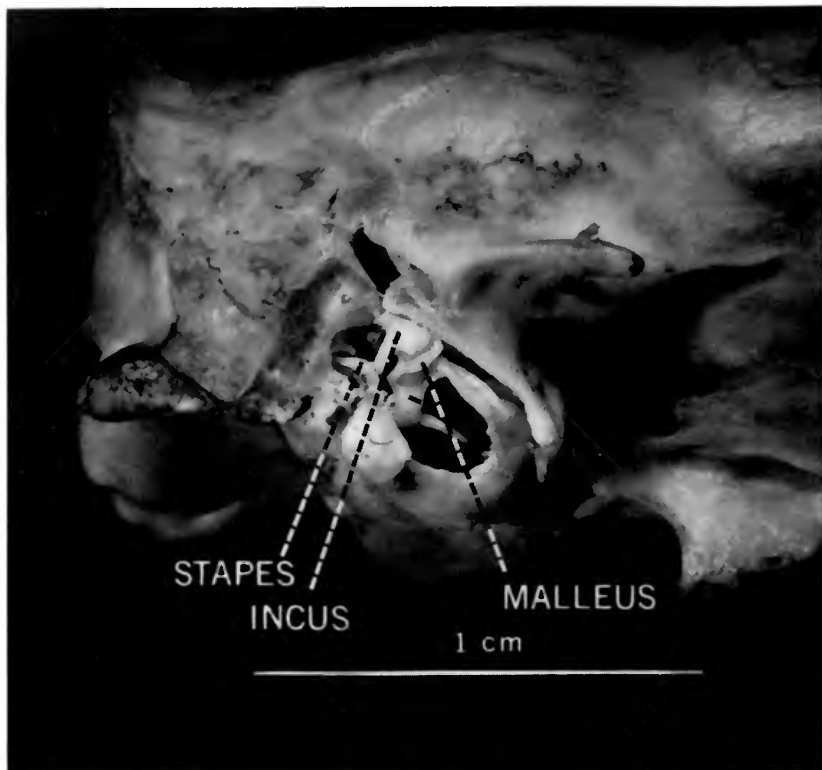


FIG. 5. *Setifer setosus*. Latero-ventral view of right middle ear. (Obscuring bone removed.)

The stapes has a shallow head; the crura are well curved; the posterior less than the anterior. The desiccated stapedia artery occupies the anterior half of the space between them and is not in a bony enclosure. The plate is elliptical, its longitudinal axis forms an angle of about 28° with the horizontal, and the stapes ratio is about 2.0.

Nesophontes edithae

In *Nesophontes* the long stapedia axis forms with the horizontal an angle of about 30° and the stapes ratio is about 2.3.

Setifer setosus

Figure 5

The tympanic is much inclined toward the horizontal and its short recessus meatus is only slightly ascending. The wide incisura tympanica is open dorso-caudally and is covered by the squamosal. The stylohyoid lies on the lateral side of the posterior crus. The anterior crus is covered anteriorly by the tympanic process of the squamosal, further ventrally by the tympanic process of the alisphenoid. The bulla is formed to the greatest extent by the tympanic process of the basisphenoid, which covers the ventral border of the tympanic. Postero-medially, it is in sutural contact with the periotic. Anteriorly, between the tympanic ring, the ali- and basisphenoid, there is an approximately rectangular-shaped opening for the Eustachian tube. The well-developed mastoid points with its distal end in a latero- and slightly ventral direction. It is formed to a great extent by the squamosal, the rest by the periotic.

The malleus has a generalized appearance and is very similar to that of *Solenodon*. The articulation with the incus is saddle-shaped; the capitular crest sharply delineated; the long neck has a prominent hump and an apophysis orbicularis. The lamina is quadrangular.

The posterior crus incudis reaches into the epitympanic recess.

The space between the crura stapedis is wide and the stapedial artery is not enclosed in a bony canal. The ossicular functional axis angle with the horizontal is about 35°, the lever ratio about 1.2, and the stapedial ratio about 2.0.

Echinops telfairi

Figure 6

A large tympanic process of the basisphenoid forms the ventral wall of the cavum tympani and covers the tympanic from below. Posteriorly and postero-medially, it borders on the periotic. The horseshoe-shaped tympanic has a small recessus meatus and a wide incisura tympanica which opens dorso-caudally. Its posterior crus is covered laterally to a great extent by the stylohyoid. The well-developed mastoid process is flattened on its antero-lateral and ventro-medial sides and points latero-ventrally. Its larger anterior part is supplied by the squamosal, the posterior part by the periotic.

The malleus head bears a saddle-shaped articulation and its lamina is quadrangular. The angle in the neck is about 90°. The apophysis orbicularis is well developed and the narrow manubrium ends in a slender spatula.

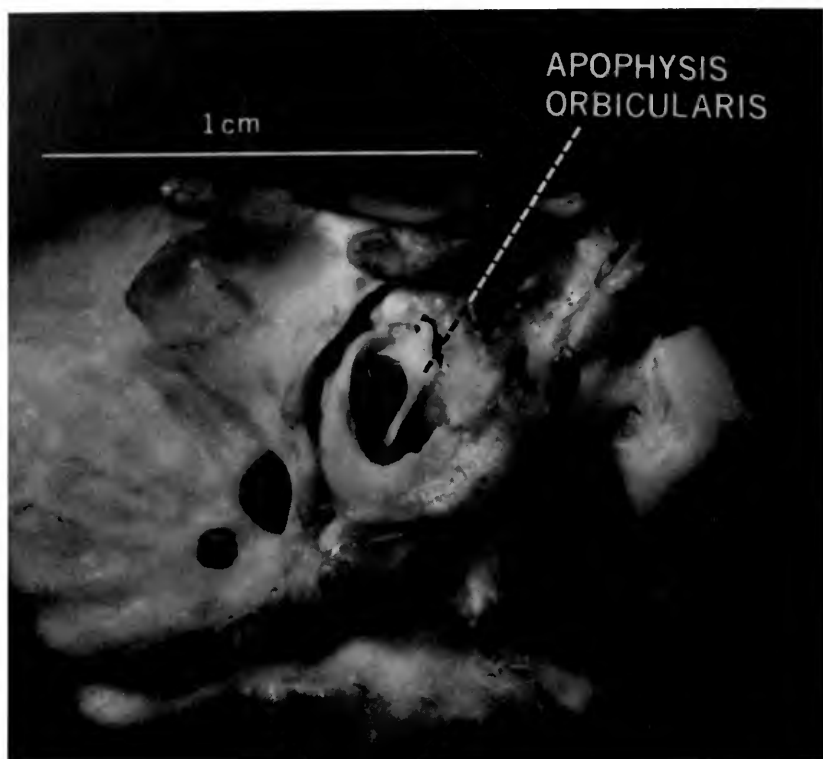


FIG. 6. *Echinops telfari*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

The incus has a robust body. Its stapedial crus is plump and does not diminish in size distally. The short crus is well developed and reaches into the epitympanic recess.

The shallow head of the stapes is oval and the crura are well arched. The angle of the ossicular functional axis with the horizontal is about 36° as in *Tenrec*. The lever ratio is 1.2 to 1.3. The stapes ratio is about 2.0. The stapedial artery is not enclosed in a bony canal and fills only a small part of the intracrusal space.

Oryzorictes niger

Figure 7

The horseshoe-shaped tympanic has a very small recessus meatus and is very little inclined from the horizontal. The small incisura tympanica is located laterally and caudo-dorsally and is filled by the

malleus. The cavum tympani is covered below by the tympanic process of the basisphenoid; the latter is in close contact and overlaps part of the tympanic ring. Posteriorly, the tympanic process of the basisphenoid is in sutural contact with the tympanic process of the periotic. The opening for the Eustachian tube is formed by the alisphenoid, the basisphenoid, and the tympanic; the opening for the carotid artery by the tympanic and periotic.

The malleus has a generalized appearance with a sharp capitular crest, a long, sharp-angled neck, a well-formed apophysis orbicularis, and a large quadrangular lamina. The posterior end of the short crus incudis reaches into the epitympanic recess. The ossicular functional axis forms an angle of about 42° with the horizontal plane and the stapes ratio is about 2.2.

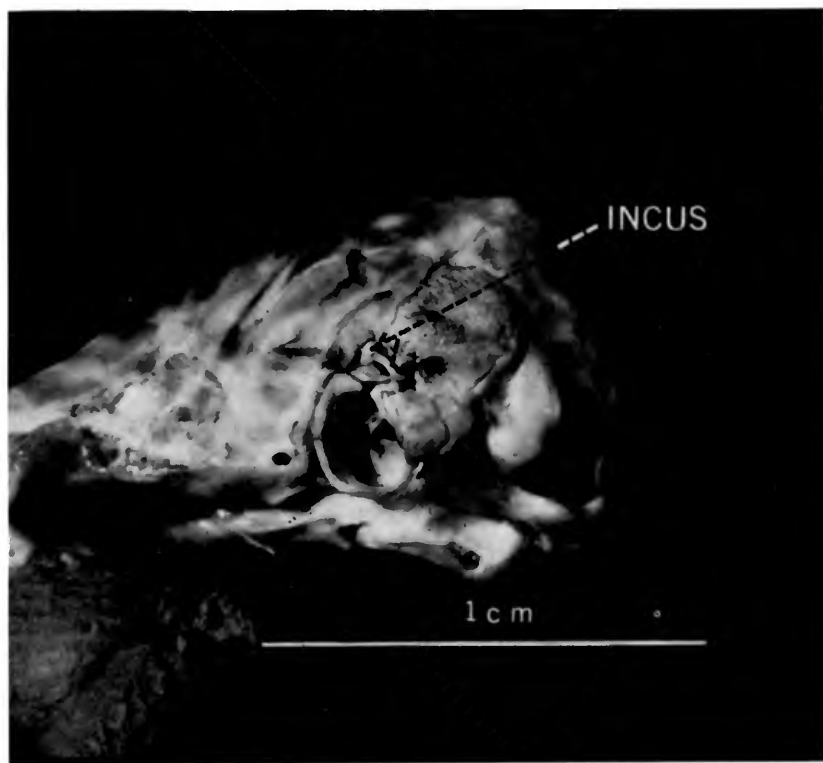


FIG. 7. *Oryzomys niger*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

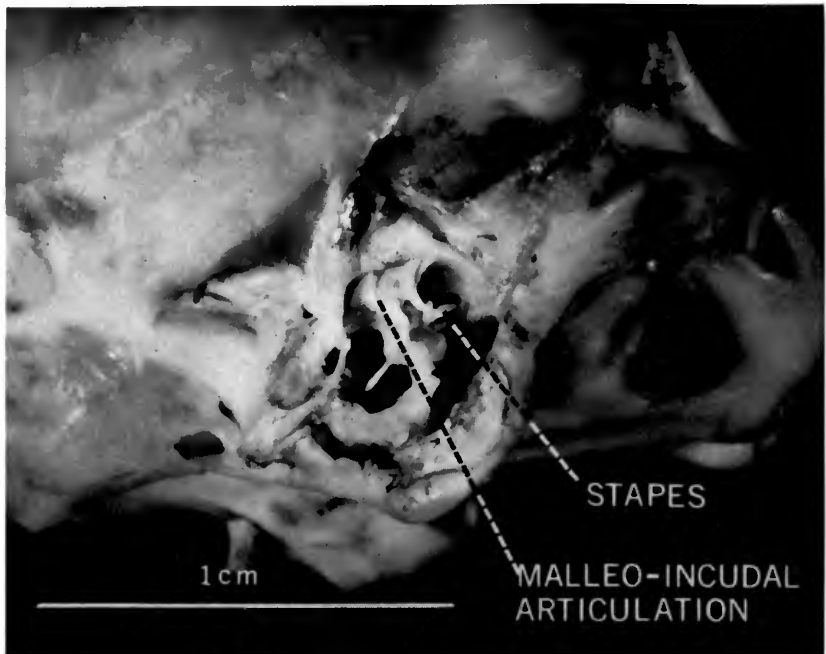


FIG. 8. *Potamogale velox*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

Potamogale velox

Figure 8

A large tympanic process of the basisphenoid covers the cavum tympani ventrally. It reaches laterally beyond the ventral edge of the ectotympanic and is not in close contact with it. The posterior crus of the tympanic is obscured from the lateral view by a post-tympanic process of the squama and further down the stylohyoid, which in turn with its ventral margin is closely attached to the tympanic process of the basisphenoid. Dorso-laterally, the stylohyoid is in contact with the tympanohyale. The opening for the carotid artery is formed by the periotic and by the tympanic process of the basisphenoid.

The neck of the malleus has a hump and a well-developed apophysis orbicularis. Its lamina is relatively small. The manubrium, shaped as in *Echinops*, is directed antero-ventrad and much mediad. The angle of the ossicular functional axis with the horizontal plane is about 40° and the stapes ratio is about 1.9.

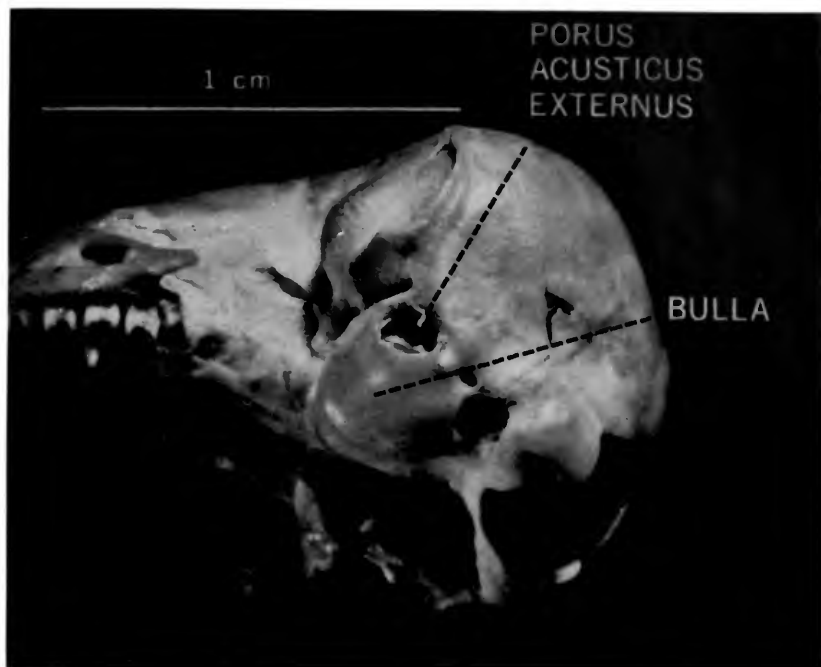


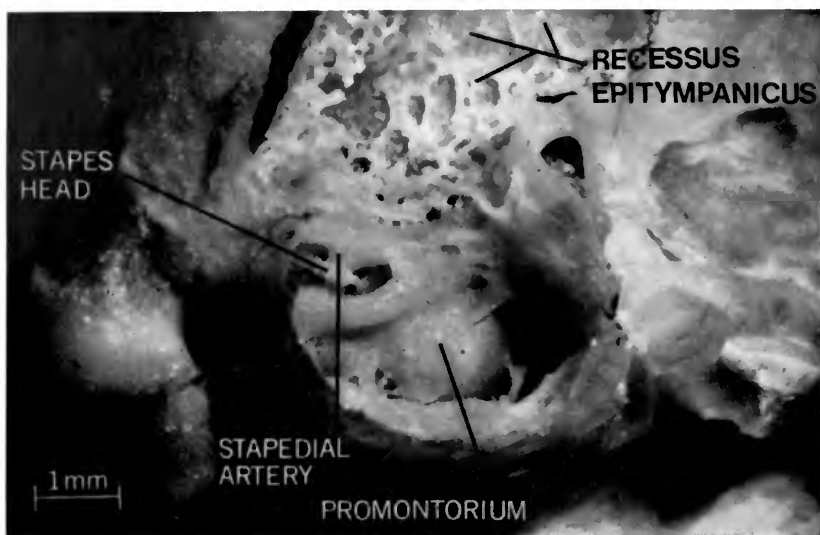
FIG. 9. *Chrysochloris (stuhlmanni?)*. Latero-ventral view of left auditory region.

Chrysochloris stuhlmanni

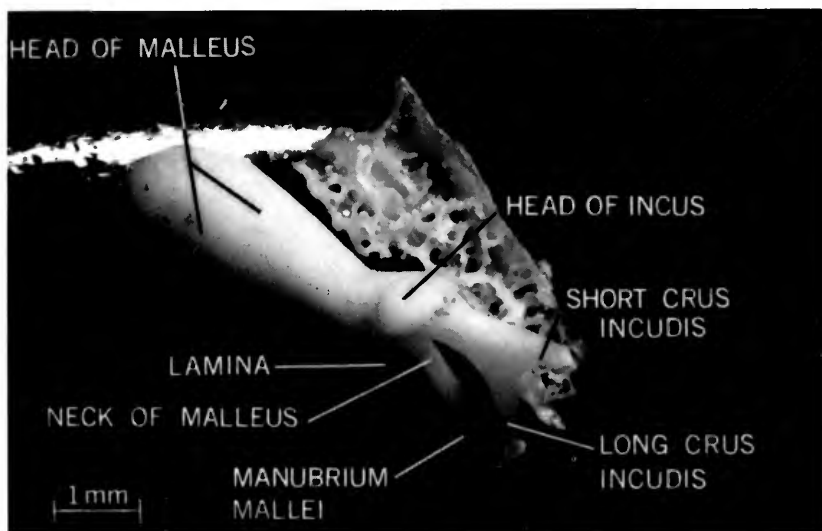
Figures 9, 10A and B

The tympanic forms a long recessus meatus which supplies a large part of the bulla. The porus externus is small and nearly round. Medial and in sutural contact with the tympanic is a tympanic process of the basisphenoid. Posteriorly, this process, the periotic, and the tympanic participate in the formation of the foramen caroticum. The configuration of the external ear of the *Chrysochloris* shows a great similarity to that of *Talpa* and *Notoryctes*. This apparently is due to adaptation to their common environment.

The unusual shape and position of the malleus and incus attracted the interest of many zoologists and I refer to the description by Doran (1877, p. 37). Doran did not find a lamina and speculated on its presence. The specimen studied shows a well-developed, thin, triangular lamina (fig. 10B). The ossicles deviate in their morphology greatly from those of all other insectivores. The stapes, however, has kept its insectivorous character with its well-curved crura between



A



B

FIG. 10. *Chrysochloris (stuhlmanni?)*. A. Latero-ventral view of right middle ear. (Obscuring bone, malleus, incus removed.) B. Medio-caudal view of right malleus and incus.

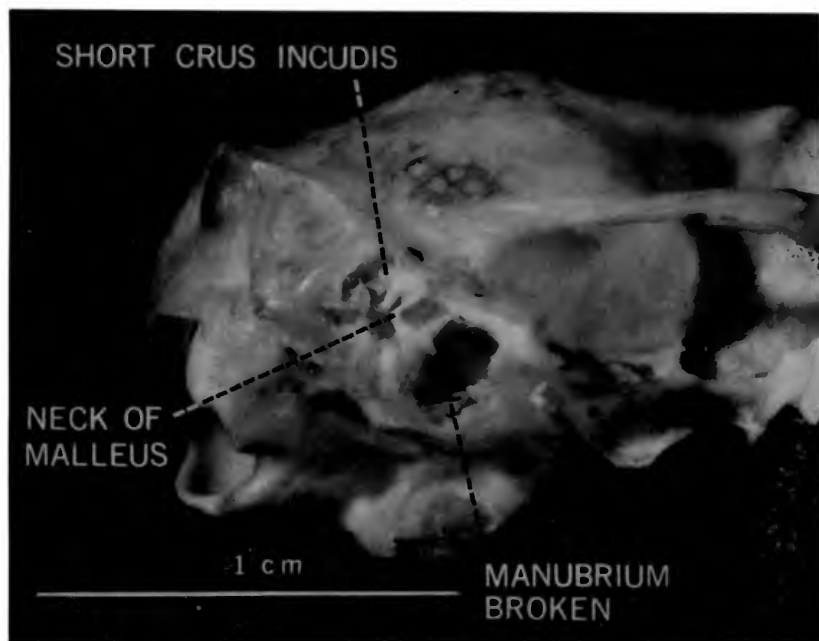


FIG. 11. *Hylomys peguensis*. Latero-ventral view of right middle ear.

which the stapedia artery passes, enclosed in a bony canal, as in *Talpidae*. The stapedia ratio is about 2.0.

Hylomys peguensis

Figure 11

The tympanic is horseshoe-shaped with a small, only slightly ascending, recessus meatus. The eardrum is very much inclined toward the horizontal. The dorsal end of the anterior crus is bent dorso-caudad. At the bend of the crus originates a short horn-like process which points antero-ventrad. The large tympanic process of the basisphenoid reaches slightly lateral of the ventral edge of the tympanic. Caudally, it is in sutural contact with the tympanic process of the periotic. The foramen caroticum is bordered by the tympanic process of the basisphenoid, the tympanic process of the periotic, and the ectotympanic. The opening for the Eustachian tube is bordered by the tympanic, the tympanic process of the basisphenoid, and the alisphenoid.

The malleus has a saddle-shaped articulation. The neck forms an angle of about 90° , its wide lamina is quadrangular and the apoph-

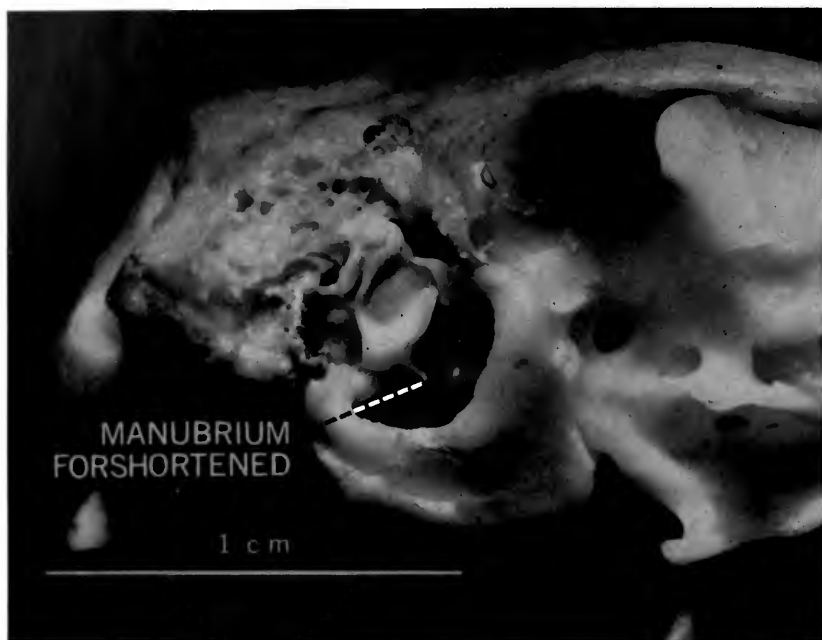


FIG. 12. *Erinaceus europaeus*. Latero-ventral view of right middle ear. (Obscuring bone removed.)

ysis orbicularis is well developed. The short manubrium is flat on its antero-dorsal and postero-ventral side and its distal end is spatulated.

The incus is robust. Its posterior crus reaches into the epitympanic recess and the ossicular functional axis forms an angle of about 27° with the horizontal. The processus lenticularis of the stapedial crus incudis articulates with the shallow caput stapedis.

The stapedial crura are very curved and the elliptical stapes plate has a ratio of 1.9. The stapedial artery passes between the crura in a broad, open, bony trough. The lever ratio is about 1.0.

Erinaceus europaeus

Figure 12

The ectotympanic which has a long recessus meatus is inclined very little from the horizontal. The tympanic cavity is covered ventro-medially by a large tympanic process of the basisphenoid which reaches laterally slightly beyond the ventral edge of the tympanic. Anteriorly, together with the ectotympanic and the alisphenoid, it surrounds an irregularly-shaped opening for the Eustachian tube.

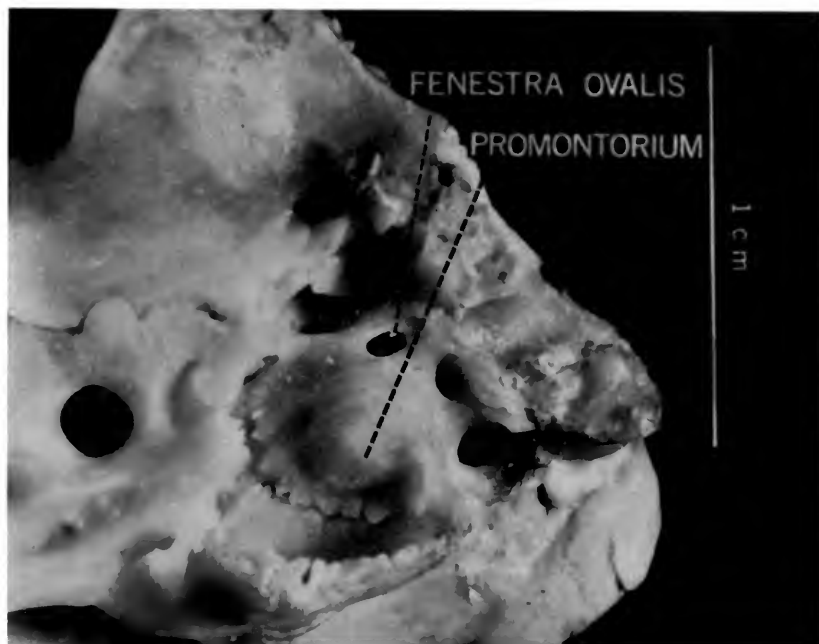


FIG. 13. *Erinaceus europaeus*. Latero-ventral view of left periotic.

Posteriorly, it is in sutural contact with the periotic. In some specimens a stylohyoid obscures the lateral view of the posterior crus of the ectotympanic. The dorsal end of the posterior crus is in contact with the tympanohyale. The large opening for the carotid artery is formed by the tympanic and the periotic. The mastoid process, formed by the periotic, points ventro-laterally.

The malleus has a saddle-shaped articulation. Its long neck is only slightly curved. The lamina is quadrangular and the apophysis orbicularis is only indicated. The manubrium which is severely bent medially, but only slightly antero-ventrally is foreshortened in the figure. The short crus incudis reaches into a fossa incudis in the posterior wall of the cavum tympani. The ossicular functional axis angle with the horizontal is about 20° . The stapedial crus incudis is stout and equal in size along its whole length. The crura are well curved and the artery is not enclosed in a bony canal. The plate is elliptical and the stapedial ratio is about 2.0 (fig. 13).

Hemiechinus auritus

The auditory region is so similar to that of *Erinaceus* that a separate morphological description seems to be unnecessary. The or-

bicular functional axis angle with the horizontal is about 20° and the stapedia ratio is also about 2.0.



FIG. 14. *Ictops dakotensis*. Latero-ventral view of left periotic.

Ictops dakotensis

Figure 14

A specimen of *Ictops* is available to me in which the periotic with the fenestra ovalis is preserved. The stapedia ratio is 2.0, exactly as in *Erinaceus* (fig. 13).

Elephantulus renatus

Figure 15

The tympanic forms a recessus meatus and a cylindrical ear canal which is directed latero-caudad. The membrana tympani approaches the vertical plane. Medially to the ectotympanic and clearly demarcated from it on the base of the skull is a large entotympanic (Van Kampen, 1905), which contributes the medial and largest part of the bulla. The alisphenoid process together with the squamosal forms the anterior wall of the bulla. The Macroscelidae differ from most

of the insectivores in that the basisphenoid does not participate in the bulla formation. Postero-medially, the entotympanic borders

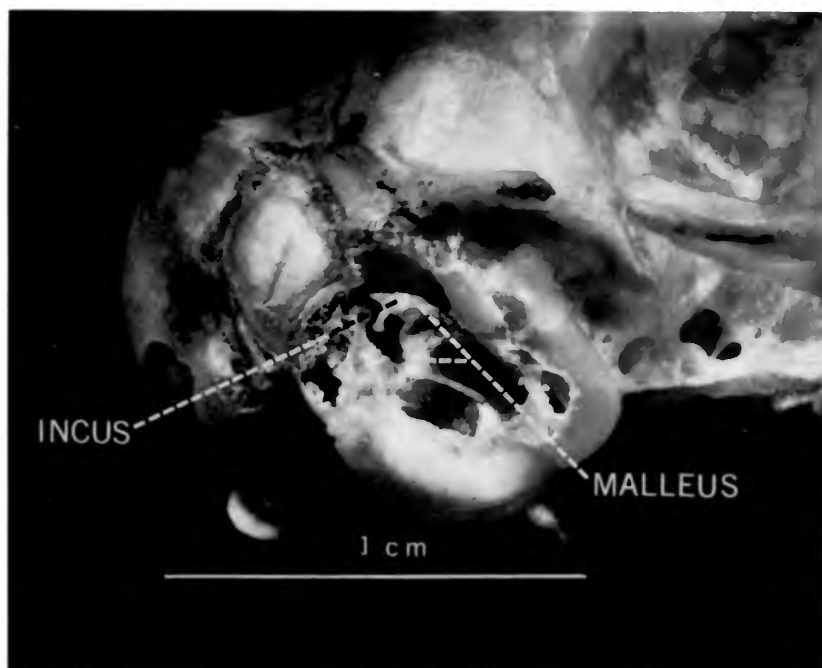


FIG. 15. *Elephantulus renatus*. Latero-ventral view of right middle ear. (Obscuring bone removed.)

the periotic, which participates also in the formation of the bulla. Posteriorly, the entotympanic and the periotic border the foramen caroticum.

The articulation of the malleus is saddle-shaped. Its neck is long and moderately curved. The apophysis orbicularis is well defined; the lamina relatively small; and the manubrium is directed antero-medial and only slightly ventrad. The angle of the orbicular functional axis with the horizontal measures about 20° . In *Nasilio* this angle is also 20° . The distal end of the short crus incudis lies in a fossa in the posterior wall of the cavum tympani.

The stapes has little curved crura. The stapedia artery lies in an open bony trough. The anterior part of the stapedia plate is wider than the posterior and the stapedia ratio is about 2.0.

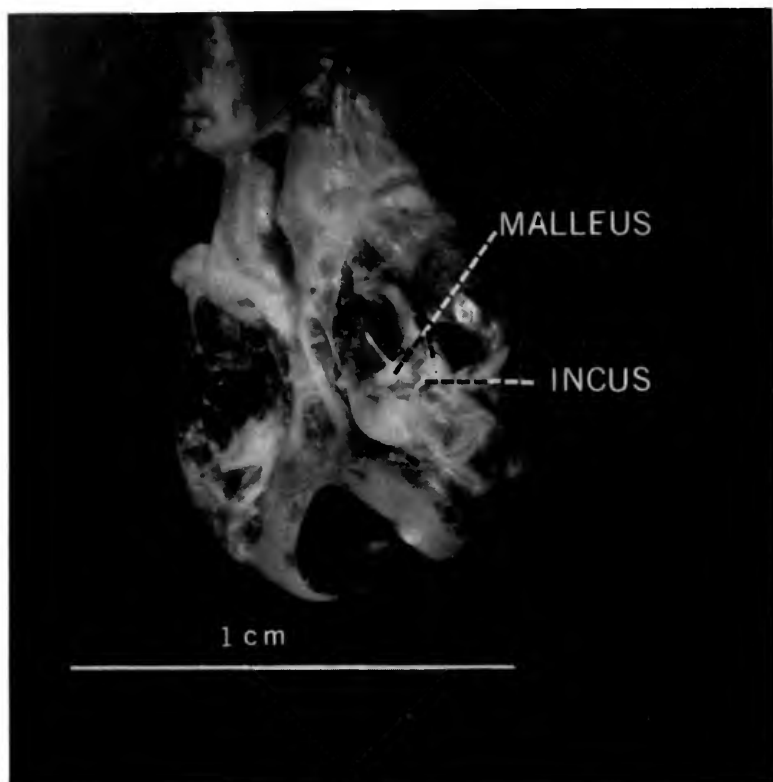


FIG. 16. *Sorex veraespacis*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

Sorex veraespacis

Figure 16

The middle ear is located on the base of the skull. The tympanic forms a nearly complete ring. The minute incisura tympanica is open latero-caudally due to the unusual position of the middle ear. The tympanic is not covered from below and its widest part is antero-medially. Medially, the middle ear is open. The tympanic ring with the membrana tympani is in a nearly horizontal plane and most of the periotic is located caudally from them.

The malleus and incus are of the generalized type. The articulation is saddle-shaped. The long neck has a bend of about 90°. The large, thin lamina is quadrangular and the apophysis orbicularis is large. The thin manubrium is straight and the spatula at the distal end is very slender.

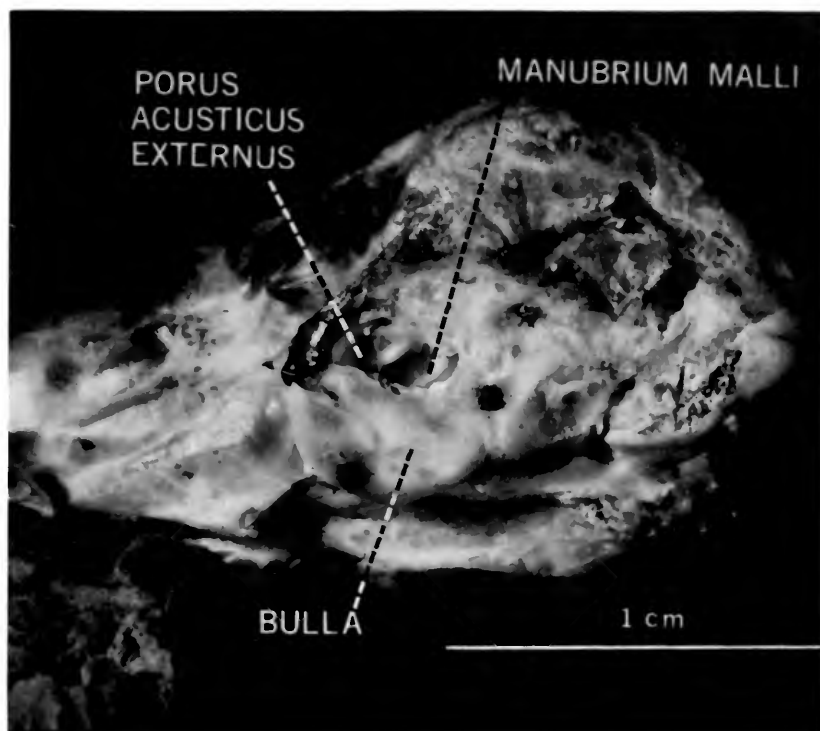


FIG. 17. *Talpa europaea*. Latero-ventral view of right auditory region.

The posterior crus incudis is very short and blunt. The stapedial crura are well curved and the stapedial ratio is about 2.0. The artery is not enclosed in a bony canal.

Blarina and *Crocidura* (stapedial ratio is 2.0) are very similar to *Sorex* and will not, therefore, be separately discussed.

Talpa europaea

Figure 17

The tympanic forms a long recessus meatus, which ascends only slightly laterally. The membrana tympani is only little inclined from the horizontal. Medial to the tympanic is a tympanic process of the basisphenoid, which borders posteriorly on the basioccipital, posterolaterally on the tympanic process of the petrotic. The oval-shaped porus acusticus externus is small.]

The articulation of the malleus is much flatter than in most other insectivore families (fig. 18). The lamina is triangular and laterally

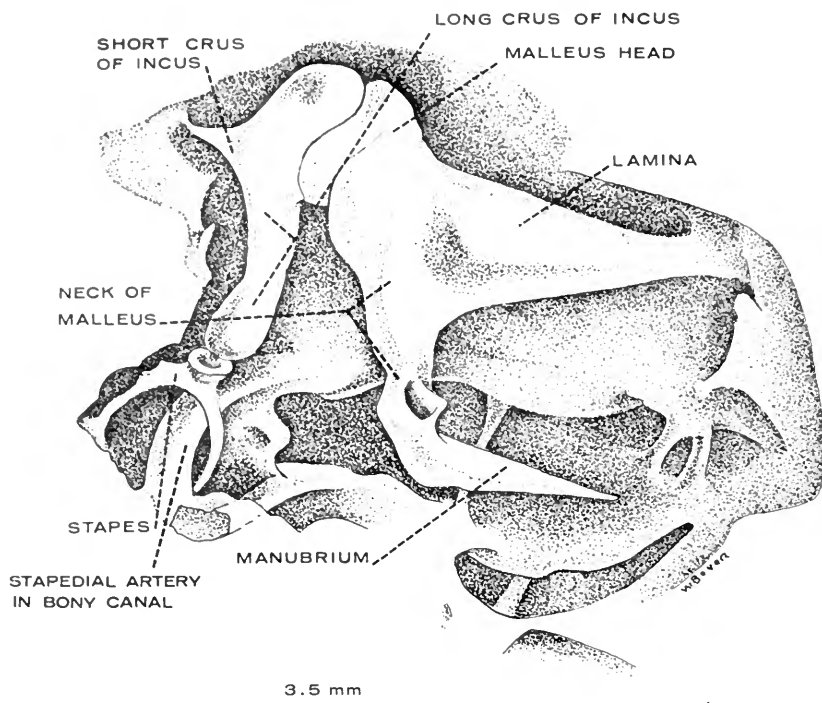


FIG. 18. *Talpa europaea*. Latero-ventral view of right middle ear. (Obscuring bone removed.)

convex. The straight neck is directed ventrad and slightly anteriorly and has no apophysis orbicularis. There is a short, curved, horn-like processus brevis mallei. The manubrium points antero-mediad.

The short crus incudis is finger-like and the stapedial crus is plump and has a cavity antero-medially. The ossicular functional axis is about parallel to the horizontal ($+2^\circ$) and the lever ratio is about 1.3 to 1.5.

The stapes has a shallow elliptical head. The crura are very curved and between them runs the stapedial artery enclosed in a bony canal. In *Talpa* it fills almost half of the distance between the crura; in *Scapanus*, nearly the whole distance. The stapedial ratio in *Talpa* is about 1.8.

The auditory region of *Scapanus townsendi* and *Scalopus aquaticus* are very similar to *Talpa* and, therefore, will not be described separately.

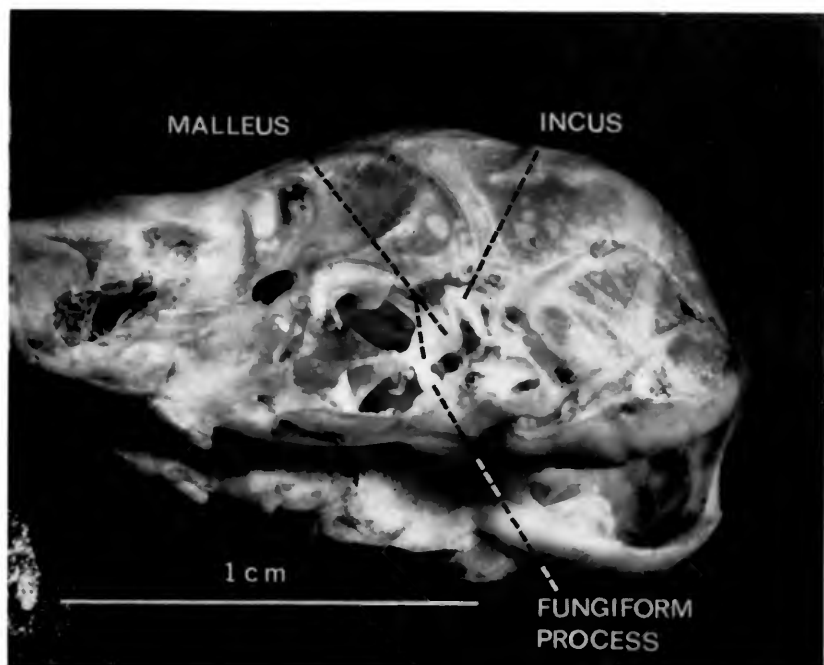


FIG. 19. *Condylura cristata*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

Condylura cristata

Figure 19

The ectotympanic forms a recessus which is much shorter than in *Talpa*. The upper end of the anterior crus is bent sharply caudad and lies against the superficies meatus. The incisura tympanica is open dorso-caudally. The membrana tympani is a little inclined from the horizontal. The ventral wall of the cavum tympani is formed by the tympanic process of the basisphenoid. The postero-medial edge of the latter borders the basioccipital; on its posterior edge, the exoccipital; on its postero-lateral, the tympanic process of the periotic; and on its lateral edge, the ectotympanic. Anteriorly, the basisphenoid forms together with the tympanic and the tympanic process of the alisphenoid a small opening for the Eustachian tube. The opening for the carotid artery is formed by the periotic and ectotympanic.

The articulation of the malleus is saddle-shaped and the two facets form a caudally open angle of about 150° . It differs in that

respect from that of Talpinae and Scalopinae, presumably due to a different function in fossorial mammals. The tympanic plate lies in the horizontal plane and the lamina is about rectangular; triangular in *Talpa*. The neck has, in contrast to *Talpa*, a sharp-angled hump and from its distal end originates a fungiform (puffball) shaped process. Van Kampen (1905) looked upon it as an apophysis orbicularis, which served also for the insertion of the tensor tympani muscle. The bayonet-shaped manubrium points anteriorly.

The short process of the incus is better developed than in *Talpa*. The ossicular functional axis angle with the horizontal is about zero and the lever ratio is about 1.1.

The stapedia artery nearly fills the space between the crura and, as in *Talpa*, is enclosed in a bony canal. The stapedia ratio is about 2.2.

Uropsilus soricipes

Figure 20

The middle ear is located on the base of the skull similar to that in shrews. The tympanic has a well-developed recessus meatus and the membrana tympani are lying nearly in the horizontal plane. Due to the unusual position of the middle ear, the incisura tympanica opens caudo-laterally. The porus acusticus externus is wide. A tympanic process of the basisphenoid covers the lower part of the cleft on the medial side of the cavum tympani between the tympanic resp. membrana tympani and the dorsal wall of the cavum tympani. This process is not present in *Sorex*. The greatest part of the periotic is caudal to the middle ear, as in *Sorex*. Antero-medially, between the ali-, basisphenoid, and the tympanic, is the opening for the Eustachian tube.

The articulation of the malleus is saddle-shaped; the long neck has a marked hump. The thin lamina is quadrangular and the apophysis orbicularis is well developed. The manubrium points antero-ventrad and much mediad. The posterior crus incudis is short and the stapedia crus diminishes distally in size. The angle of the ossicular functional axis with the horizontal amounts to about 5°. The stapedia ratio is about 2.0. The stapedia artery runs in an open trough.

Tupaia palawanensis

Figure 21

The bulla is formed to the greatest extent by a large entotympanic. Its longest axis runs from caudo-lateral to antero-medial.

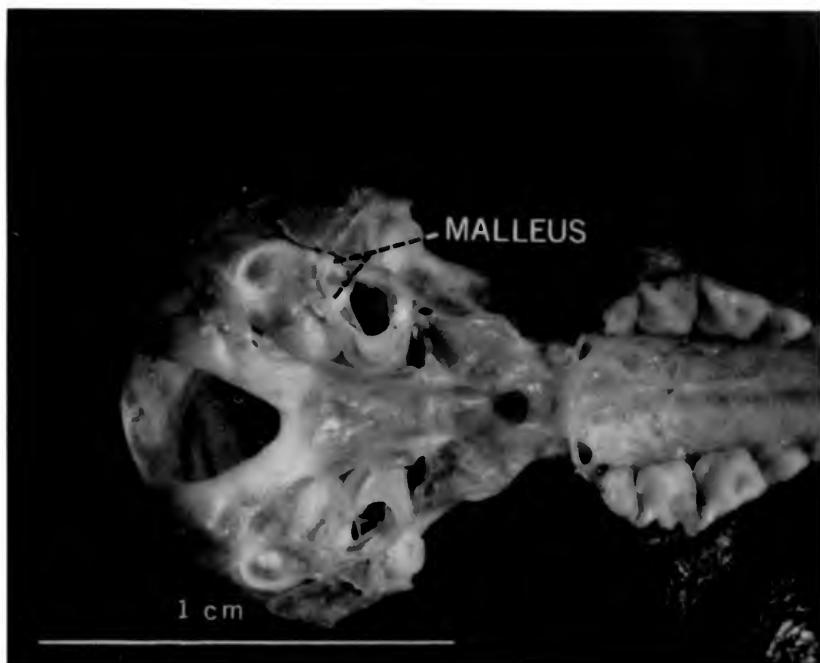


FIG. 20. *Uropsiles soricipes*. Latero-ventral view of left middle ear. (Obscuring bone removed.)

Medially, it borders the basisphenoid and the basioccipital and postero-laterally, the mastoid. Neither the basisphenoid nor the alisphenoid participate in the formation of the bulla. The entotympanic forms a recessus meatus and a short cylindrical ear canal. The small horseshoe-shaped tympanic is only loosely attached to the inside of the entotympanic, which obscures the tympanic from the lateral view to a great extent.

The head of the malleus and the incus reach into the recessus epitympanicus. The anteriorly-pointed head of the malleus has a saddle-shaped articulation and is sharply bent medially, forming with the manubrium an angle of about 115° . The anterior process is short, its lamina is very small. The processus brevis mallei is prominent due to the sharp angle of the head with the manubrium. The latter has a blunt lateral edge and is directed ventrally and very slightly anteriorly.

The body of the incus is robust, its posterior crus very well developed, being nearly as long as or even longer than the stapedial crus.

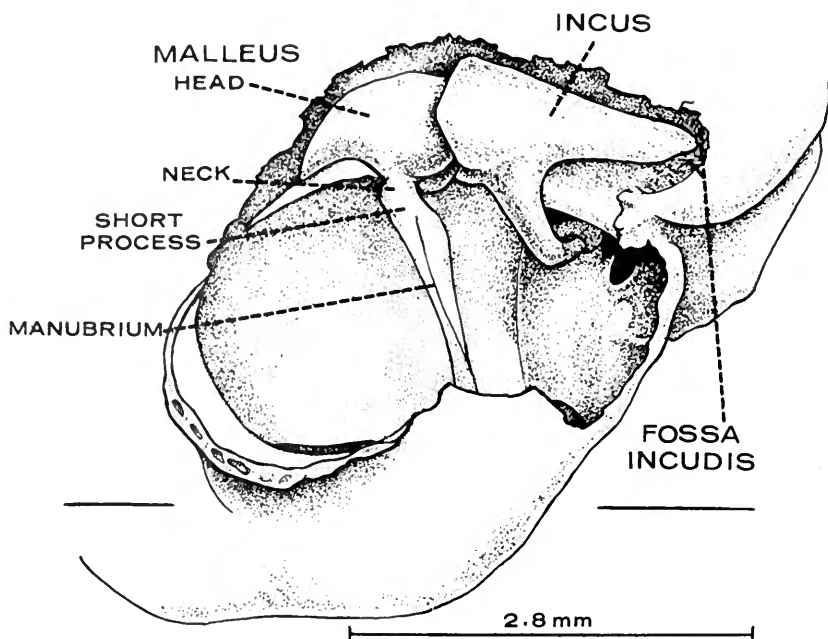


FIG. 21. *Tupaia palawanensis*. Lateral view of left middle ear. (Obscuring bone removed.)

It reaches into the fossa incudis in the posterior wall of the cavum tympani.

The stapedial crura are only slightly curved and form an oval foramen which is nearly filled by the large stapedial artery. The latter is enclosed in a bony canal, which is interrupted between the crura.

The foramen for the carotid artery is formed postero-medially by the periotic, which comes in the form of a short, small strip to the ventral surface of the skull. The rest of the circumference is supplied by the entotympanic.

The angle of the ossicular functional axis with the horizontal is about $+5^\circ$. The very elongated stapedial plate has a ratio of about 2.9, which is greater than that in any other insectivore examined.

DISCUSSION

ECTOTYMPANIC, ENTOTYMPANIC, AND TYMPANIC PROCESS OF THE BASISPHENOID

The auditory region undergoes specialization which becomes manifested in various degrees of participation of the ectotympanic

(tympanic), the tympanic process of the basisphenoid, and the entotympanic in the formation of the bulla and in the degree of complexity to the organization of these elements.

There is no recessus meatus in the primitive auditory regions of *Sorex* and hardly any in *Solenodon*. In all other genera a recessus meatus is present. With progressive specialization of the auditory region the recessus increases in size.

A tympanic process of the basisphenoid is not present in *Sorex* and *Solenodon*. *Didelphis*, among the marsupials, corresponds to some extent with this degree of differentiation. There is, however, already a partial cover (alisphenoid) anteriorly on the ventral side of the cavum tympani. All other insectivore genera have a tympanic process of the basisphenoid with the exception of *Macroscelides* and *Tupaia*, where it is supplanted by an entotympanic. The tympanic process extends in most genera from the midline to lateral of the ventral edge of the ectotympanic. In the generalized genera, as in *Potamogale*, it has no contact with the ectotympanic on the macerated skull. In the specialized genera, as in *Erinaceus*, it turns around the ventral edge to the lateral side of the ectotympanic and the two structures can easily be separated. In the Talpidae and Chrysochloridae the tympanic process of the basisphenoid is in sutural contact with the ectotympanic.

The presence of an entotympanic is not characteristic for either order. It is found in several families of marsupials, as well as insectivores, and increases in size with progressive specialization of the auditory region. There is none in *Sorex* and *Solenodon*; a large one in *Macroscelides*; and the largest in *Tupaia*. Similarly, among the marsupials, *Didelphis* has a very small entotympanic and *Dromiciops* a large one.

OSSICLES

Like the structures discussed above, the ossicles also exhibit various degrees of specialization. This applies mostly to the malleus, less to the incus, and relatively little to the stapes.

MALLEUS

The malleus shows greater variation in its morphology than the incus. This agrees with my observation in the marsupials. In the latter it was possible to show the interrelationship between the tympanic and the malleus and explain them with their common ontogeny

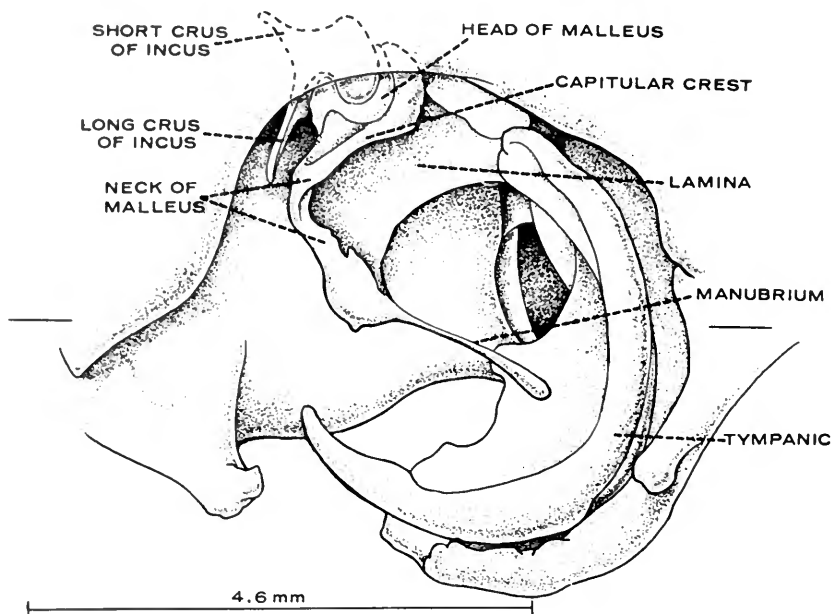


FIG. 22. *Didelphis albiventris*. Lateral view of right middle ear.

and their close mechanical relationship. The changes in the tympanic are probably primary due to its greater exposure to outside mechanical forces; those of the malleus secondary (Segall, 1969 b). A similar situation prevails in the insectivores. The malleus has a generalized form in the majority of the genera. The articulation is saddle-shaped, except in the Talpidae, Scalopinae, and Chrysochloridae, where it is much flatter.

The neck of the malleus is long and shows a sharp bend in the generalized forms. In the more specialized Erinaceidae, the bend is reduced to a slight curve. The Talpidae have a nearly straight neck and in the Tupaiidae, the neck is practically missing.

The lamina is large, thin, and quadrangular in the generalized genera. In the Talpinae it is much smaller, triangular, and laterally convex. In *Condylura* the lamina is somewhat rectangular, different from that in *Talpa*. The malleus of *Tupaia* has a very small lamina only. The reduction in the size of the lamina is approximately paralleled by the reduction in length of the neck.

The apophysis orbicularis is well developed in the generalized forms; becomes sessile, then indistinct in the more specialized genera; and finally disappears altogether. This can be well observed in the

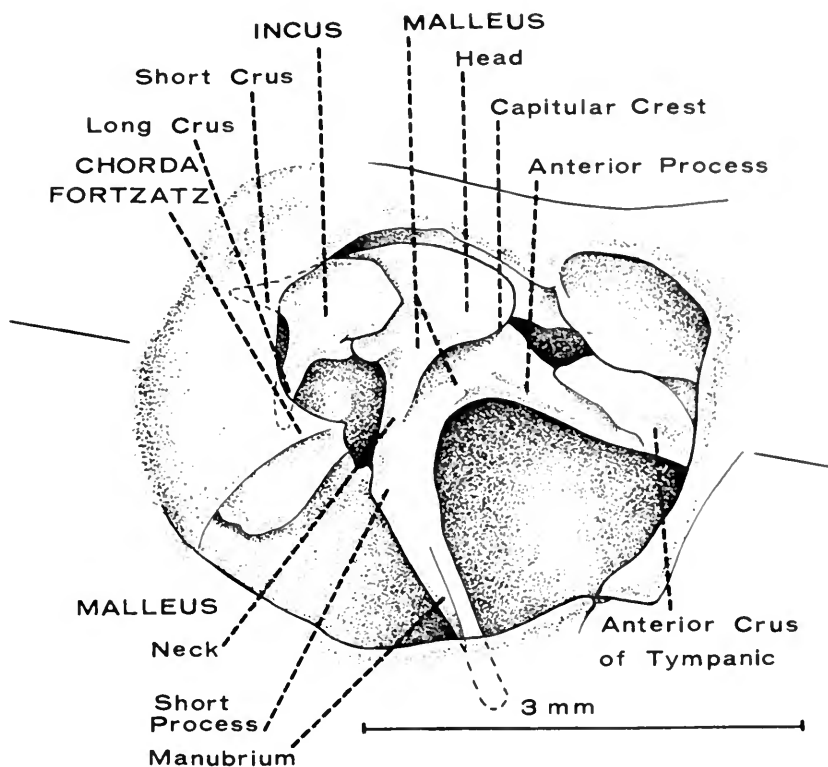


FIG. 23. *Dromiciops australis*. Lateral view of right middle ear.

Erinaceidae, where *Hylomys* and *Echinosorex*, which represent the more generalized genera, have a well-developed apophysis orbicularis while the more specialized *Erinaceus* and *Hemiechinus* have only an indication of it. There is none in the Talpidae. The disappearance of the apophysis orbicularis goes parallel with the straightening of the neck. A similar condition of the lamina and apophysis orbicularis can be seen in the marsupials (Segall, 1969b).

The angle between the neck and manubrium is antero-ventrally and slightly medially directed in some families. In *Erinaceus* and *Hemiechinus* the angle is open antero-ventrally and very much medially. In *Tupaia* the membrana tympani with the manubrium stands in a nearly vertical plane and the head of the malleus is severely bent medially against the latter.

The mallei in both orders with very generalized auditory regions, as in *Solenodon* (fig. 4) and in *Didelphis* (fig. 22), are very sim-

ilar to each other. The same applies to genera with very specialized auditory regions like those in *Tupaia* (fig. 21) and *Dromiciops* (fig. 23.)

INCUS

The incus shows, in general, few morphological differences in the various families. The posterior crus is short in the generalized taxa and its posterior end rests in most genera in the epitympanic recess; only in the most specialized ones does it reach into a fossa incudis in the posterior wall of the cavum tympani. The modification of the incus in the fossorial genera is striking. This can be seen in the insectivores (*Talpa*, fig. 18 and *Chrysochloris*, fig. 10b) as well as in marsupials (*Notoryctes*, figs. 3, 3A).

The position of the short crus is a determining factor in the direction of the ossicular functional axis (see *Methods* and *Material*). The angle between the ossicular functional axis and the horizontal plane tends to be greater in the generalized forms. Viewed from the right side, the axis turns with increased specialization counterclockwise and the angle with the horizontal plane becomes successively smaller and even negative (fig. 24). A similar turning of the ossicular functional axis can be observed in the marsupials (Segall, 1969 b).

At a certain stage of rotation of the ossicular functional axis a change in the morphology of the malleus takes place. This is presumably a phyletic response to changing mechanical requirements. In *Hylomys*, where the angle of the axis with the horizontal is already reduced to about 27°, the malleus has still preserved its generalized form. In *Erinaceus* and *Hemiechinus*, however, where the angle is reduced to about 20°, the malleus shows morphological changes. These changes become marked when the angle comes close to the zero point, as in *Talpa*. This is especially true in *Tupaia* in which the differentiation of the malleus is similar to that of the primates. A similar condition occurs in *Dromiciops* among the marsupials (Segall, 1969 a).

The similarity among fossorial genera applies to the external appearance of the auditory region and to the articulation between malleus and incus. Both characters are presumably correlated by a modified function in subterranean environment.

STAPES

The insectivore stapes does not change to any extent with progressive specialization of the auditory region, in contrast to malleus and incus. Even in the highly specialized Talpinae and still more in

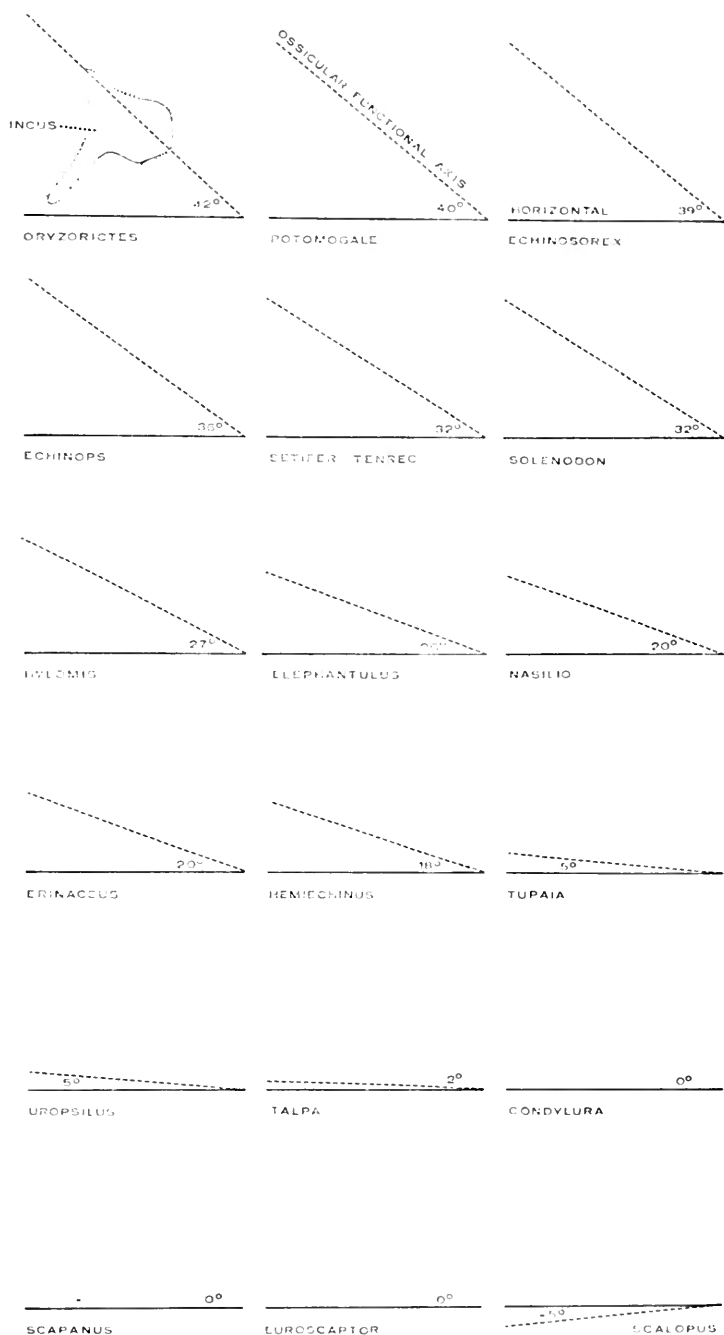


FIG. 24. The angle of the ossicular functional axis with the horizontal plane in insectivores.

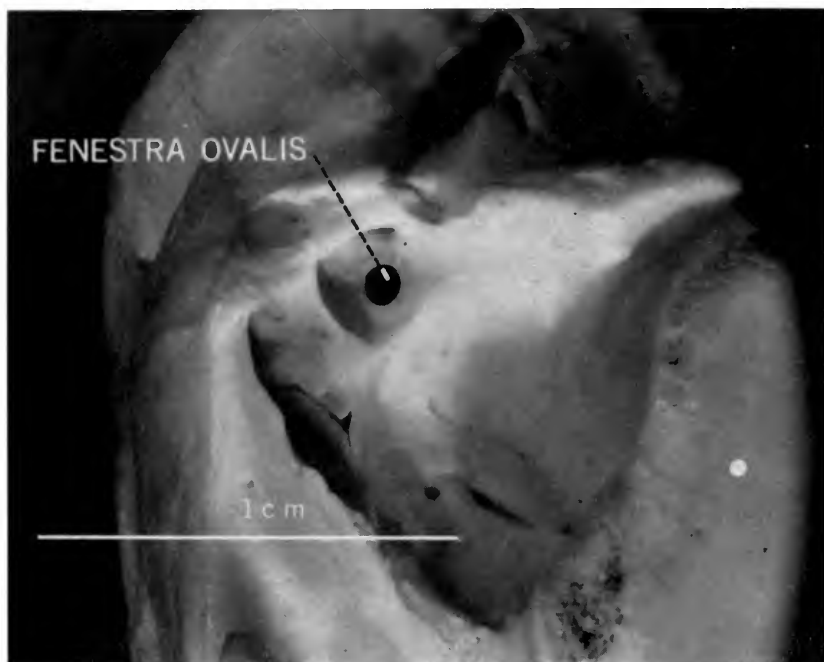


FIG. 25. *Tachyglossa aculeata*. Ventral view of periotic.

the Chrysochloridae, where the malleus and the incus have a unique morphology, the stapes does not differ from that of other insectivores. The near constancy of the stapes ratio of the plate (or the fenestra ovalis) is of taxonomic interest, especially in fossils.

Furthermore, the position of the plate or the fenestra ovalis, with regard to the horizontal plane is of comparative anatomical interest in closely related forms. Both the position and the shape of the stapedial plate can contribute to the identification of fossils. For example, the foramen ovale of the fossil erinaceoid genus *Ictops* (fig. 14) has a stapedial ratio and position identical to those of *Erinaceus* (fig. 26).

A primitive form of mammalian stapes is found in the monotremes. This type of stapes has a columella without opening (stapedial foramen) and a circular plate (stapes ratio 1.0, fig. 25). The marsupials, in which some genera approach the monotremes in this respect while others are much advanced, have stapedial plates with ratios ranging from 1.1 to 2.1. With progressive specialization of the auditory region the stapes ratio increases in marsupials (fig. 26).

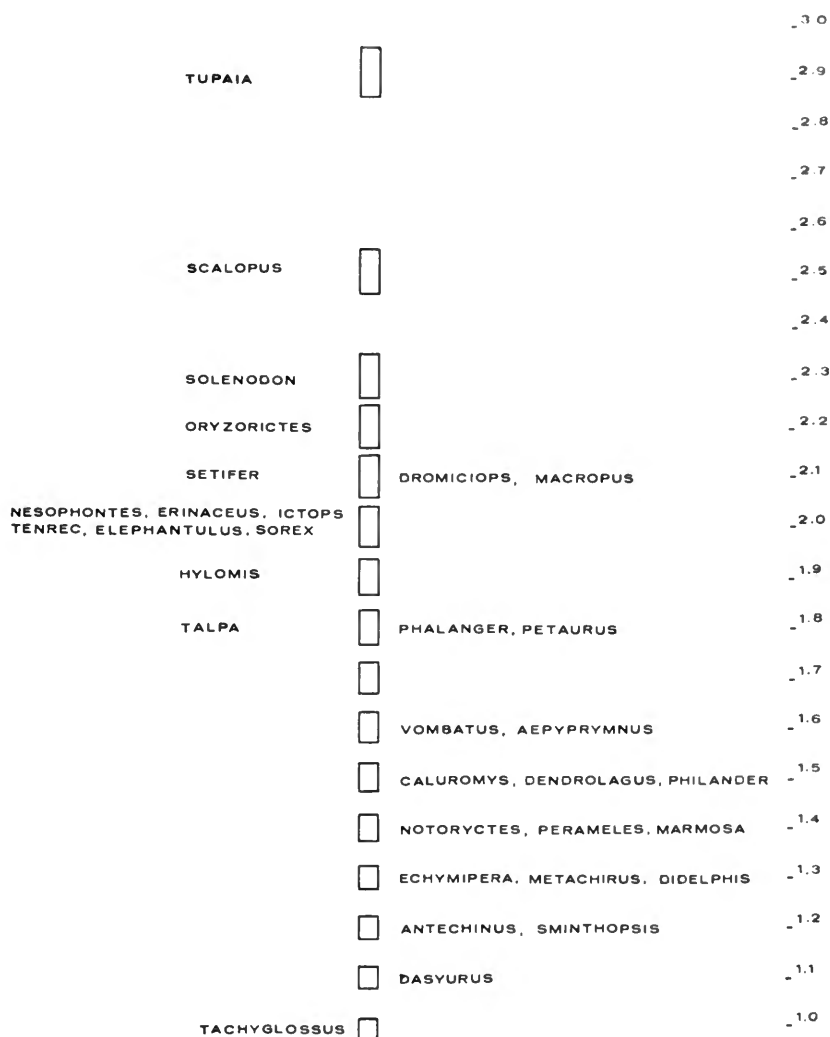


FIG. 26. The stapedial ratio: *a*, in monotremes (below); *b*, in marsupials (right side); *c*, in insectivores (left side).

At the same time, the space between the crura (absent in the columella-like stapes) enlarges only slightly in the marsupials, while the stapes plate may expand considerably. The stapedial foramen in marsupials, if present at all, is always small and never reaches the size commonly observed in insectivores.

In *Notoryctes* the malleus and incus have a morphology that is quite different from that of any other marsupial (fig. 3). The stapes, however, retains its marsupial character. It has a flat columella with a shallow groove at the base, but no canal. Specialization of malleus and incus, but not of the stapes, may be related to the fossorial habit of *Notoryctes*. The same two elements are modified in fossorial insectivores (Talpinae and Chrysochloridae), while the stapes retains its typical insectivore character.

The morphology of the stapedia plate changes first, that of the crura afterward. It is presumably the function that determines the configuration of the plate. The presence, absence, or degree of development of the stapedia artery is not directly correlated with the size of the opening between the crura and it only occasionally fills it completely.

The round shape of the plate and fenestra ovalis is a primitive mammalian character; the elliptical shape, a specialized one.

The present study has shown that the stapes is characteristic in each of the two orders of mammals considered. In the marsupials there is a progressive specialization of the stapes from a columella-like form with a round plate to a stapes with a small opening between the crura and an elliptical plate, while in the insectivores it is invariably stirrup-shaped, irrespective of the general level of specialization of the genus.

In contrast, the ectotympanic, malleus, and incus in both orders show similar, parallel, progressive morphological changes with overall increase of specialization of the genera.

In both orders, furthermore, fossorial genera show marked deviations from the typical condition of malleus and incus, but not of the stapes. It was suggested that these profound changes are related to the fossorial habits.

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